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## Time-frequency domain EEG activity during the preparation of task sets and movements

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## Chapter 3

# Discussion

## 3.1 Discussion of results

As summarized below, the various contrasts, fast - slow, switch - hold, left - right hand, as well as cue types, were associated with differences in the time course of the LRP, instantaneous amplitude and phase locking, and lateralization in those measures.

### 3.1.1 ERP's

In the ERP's, an increased post-cue positive peak, lasting from around 300 to 600 ms post-cue, was found for the following cue conditions. First, in the cued chiasitic switching study (section 2.3), when the cue was different than the previous cue, the peak was greater. This effect determined the grouping of conditions at frontal - central channels, e.g. the switch - hold and hold - switch sequences grouping together. At parietal - occipital channels, there was a further effect of switching, switch cues being followed by a more positive peak than hold cues. Given a cue- and task-switch, a greater peak preceded fast than slow responses. Second, in the sequence cueing task (section 2.5), cues providing both elements of the sequence had a greater parietal - occipital peak. Third, when cueing response hand in the choice / go - no go task (section 2.6), hand cues showed a greater peak than neutral cues. Taking the results together, the post-cue peak appears to reflect what is done with information contained in the cue. Note that a switch and a hold cue contain the same amount of information - one bit, reducing the uncertainty in a set of two equally probable events. So, the peak does not reflect how much information is in the cue, but how much or what kind of activity is caused by that information within the first half second post-cue. This seems consistent with ERP studies showing task-related effects, e.g. of the task-relevance of stimuli, on the P3 component, as described in section 1.3.4, although the frontal distribution of long-lasting positivity does not seem to be described by either the P3a or P3b.

Later in preparation intervals, slow negative potentials were found to reflect various kinds of preparation. These potentials had the general characteristics of preparatory CNV-like components described in section 1.3.4. In the hand - modality task switching study, such potentials at frontal channels were greatest for fast alternation trials (section 2.1). In the hand-switch only study (2.4), but not significantly in the modality-switch study (2.2), alternation trials were again preceded by greater frontal negativity than repetition trials. In the cued switching task the main effects were a conspicuously weak frontal - central - parietal potential for slow hold - hold sequences, in which the least preparation would be expected and a fast - slow grouping occipitally, for the cue repetition conditions. In the sequence cueing study, single-element cues were followed by the greatest negative potential, centrally. In comparison with neutral and full-information cues, single-element cues allow only a half-finished kind of preparation: a motor program is being written, but cannot be completed. Perhaps this results in a stronger anticipation of the missing element, that is reflected in the negative potential, than the wait for the "go" signal that stimulus presentation provides when the full motor program can be specified. In the choice / go - no go task, hand cues resulted in negative potentials than neutral cues. So in these studies, negative pre-imperative stimulus potentials, with varying scalp distributions, covaried with a manipulation (e.g. cue information) or measure (reaction time) of preparation.

The LRP showed a response speed by task switching interaction in the hand-modality switching task. In the choice / go - nogo task, cueing the hand to be used for an upcoming imperative stimulus resulted in a pre-stimulus LRP, that was larger when the probability of response was higher. In the sequence cueing task, a pre-stimulus LRP was found only for fully specified sequences with

different elements. When the sequence was fully specified but consisted of repeated responses, the LRP did not develop during the cue - stimulus interval until just before stimulus presentation, but then rose sharply.

### 3.1.2 Theta-band amplitude and phase locking

Pre-stimulus theta band activity was found to predict subsequent reaction times in the hand - modality alternating runs task, for both alternation and repetition trials, and the chiasitic switching task, but only in the switch - switch sequence. The lack of an effect for hold - switch sequences in the cued chiasitic switching task is an inconsistency that may be worth further study, as in the alternating runs task, the alternation trials were always part of a hold - switch sequence. The reaction-time effect for hand - modality switching consisted of higher amplitude during the response-stimulus interval for fast trials, from 500 ms post-response to stimulus presentation, as well as increased amplitude immediately after the response. The effect from 500 ms decreased from frontal to occipital sites, while the earlier effect was found only at frontal and central sites.

For both fast and slow trials in the hand - modality switching task, the overall time course was qualitatively similar, consisting of peaks around the external events (response and stimulus). In the switch - switch sequence for chiasitic switching, fast and slow trials showed a different time course, with the slow condition showing a later post-cue peak in amplitude, most clearly in the parietal - occipital region. In the fast switch - switch condition, central - parietal regions showed increased theta-band phase-locking from around 750 ms post-cue, relative to the other trial sequences, and a decrease in frontal phase locking. This phase-locking pattern is perhaps one of the most interesting results in terms of possible transient large-scale cortical states implementing task sets. Although the result needs to be replicated, some speculative hypotheses can be formulated. Since prefrontal neurons can encode past and future events (section 1.3), the low frontal phase locking may reflect the weakness of the memory of both the most recent and upcoming task set. Alternatively, the decrease in phase locking may be a form of large-scale theta-band ERD in which only a small subset of activity is allowed in some form of noise reduction. The posterior increase in phase locking may reflect the effect of memory retrieval on the cortex, as discussed in sections 1.3.1 and 1.4.3; perhaps this retrieval requires a longer period or intensity of activity to recall the correct task-set memory in the relatively unstable context of switch - switch sequences.

Modality-specific switch - hold effects in theta-band amplitude were found at occipital - parietal sites in the modality switching task. Both switch-to-visual and switch-to-auditory trials showed a pre-stimulus relative increase (or delay of post-response decay) in amplitude, but this increase persisted longer, over around 500 to 1000 ms in the response - stimulus interval, preceding visual alternation trials. The pattern over conditions and time suggested that the oscillatory activity may be part of a process of selection, as discussed further in section 3.2.2. Theta-band amplitude was found to lateralize along with hand preparation, but only in the hand-switching task and only for repetition trials. In these trials, amplitude increased over the hemisphere controlling the prepared / just used hand, during the response and for around 500 ms post-response. As this effect was the only motor-related lateralization effect outside the expected mu and beta bands, it is both interesting and in need of replication. Since the transience and timing of the effect are similar to the occipital visual-switch theta burst, the same kind of speculative interpretation may be applied. That is, perhaps multiple regions of neurons in the hand or motor area are activated, followed by competition until a relevant subset remains (see section 3.2.2). Finally, in the hand-cueing task, hand cues were followed, from 500 ms up to stimulus presentation, by an increase in frontal theta-

band amplitude, relative to neutral cues. This and the fast - slow effect in the hand - modality alternating runs task are the only theta-band effects that persisted over the whole preparation interval, and so may reflect either a preparatory state or a repeating preparatory process, e.g. noise reduction through convergence, as opposed to a transient preparatory "toggling" process.

### **3.1.3 Alpha band amplitude and phase locking**

Pre-stimulus alpha-, or mu-band motor-related lateralization was found in all relevant tasks. A modality-related effect was found in the response-stimulus interval of the modality-switching task. When an auditory trial was repeated, occipital amplitude increased from response to around 800 ms into the interval. What precisely the underlying neural activity is and what it achieves are uncertain, but would seem likely to involve thalamocortical interactions decreasing the effect of visual information on the state of associative cortex (section 1.5). A further question the effect raises is why it did not occur preceding switch trials. If the effect reflects effective preparatory activity, its absence would seem to be due to an inability or difficulty to perform that activity in the alternation context. This could be due either to just having performed a visual task, or to not yet having performed an auditory task. It seems possible that, especially because visual input was constant during the whole of the modality-switching task, that the switch away from the visual task cannot be completed pre-stimulus. In that case, the effect may reveal a mechanism by which task-set inertia (section 1.2) occurs.

In the cued chiasitic switching task, high central - parietal alpha-band phase locking was found during the second half of the cue - stimulus interval for the fast hold - hold condition. It may be important in interpreting this activity that this sequence involved a lack of change that is perhaps analogous to postural stability (section 1.6). Finally, in the sequence cueing task, full - information cues resulted in central - parietal alpha-band ERD relative to neutral cues, around 600 - 900 ms post-cue. As this was the only condition in which the full response sequence could be imaged before the imperative stimulus, the effect could reflect motor imagery, perhaps as a method to keep the motor program in mind by rehearsal.

### **3.1.4 Beta band amplitude and phase locking**

Lateralized motor-related beta-band ERD and phase-locking, especially between frontal and motor regions, were found when switching between hands, in the hand-modality and hand-only switching tasks. So, the activity that survives ERD is phase-locked to other areas, although it is not clear when that subset of activity becomes phase-locked: does phase-locking increase concurrently with ERD, or was the activity already phase locked while ERD perhaps pruned the non-phase-locked activity away? Lateralization in phase-locking and ERD do not seem to be two measures of the same process, at least not in the context of the choice - go/nogo experiment. Cueing the response hand resulted in some differences in lateralized ERD, i.e. an early low-alpha and late beta-band increase in MRAA for 100 % go blocks, while no probability effect was found on phase-locking. However, this dissociation is based on differences in statistical significance and so may be an artefact of differences in noise in the two measures. Further study is needed to better determine relationship between lateralization in phase locking and, especially, the beta band. Low beta-band (16 Hz) ERS was found around 500 ms post-cue, significantly for the 50 % but also as a trend for the 100 % go probabilities. Given the post-cue temporal context, this burst may reflect a way of the inhibition of overt responses in the face of motor-related "internal" processes. In the sequence-cueing task,

increased pre-stimulus contralateral ERD was found for fully specified, repeated-element sequences, while lateralized phase-locking was found for the left- versus right-hand cues, for all cue types. Finally, in the hand-switching task, EEG-EMG phase locking increased between the EMG channel of the hand being switched away from, and contralateral central sites. This suggests that part of switching involves "freezing" the inappropriate hand and in that way inhibiting the irrelevant task set.

Non-lateralized effects were also found in the beta band. Fast trials were preceded by beta-band ERD, over central and parietal regions, in the hand - modality switching task. In the chiasitic switching task, an increase of pre-stimulus beta-band amplitude was found preceding slow switch trials, in a switch - switch sequence. The effect is similar to the lateralized ERS in the choice / go-nogo task. In both cases, responses were not given quickly (post imperative stimulus), or at all (post-cue). Possibly, subjects were confused on some switch - switch trials, and the peak reflected preparing not to respond too quickly, when an error was likely.

Finally, beta-band ERD was found in situations in which a response could be prepared. All cues in the sequence cueing task were followed by, primarily frontal - central, beta-band ERD in the cue-stimulus interval. When cueing response hand in the 100 % go blocks, beta-band phase locking increased at the end of the preparation interval relative to neutral cues. It remains to be determined exactly what relation this ERD has with preparation. For instance, is the ERD only a consequence of changes in the brain's information processing, or does ERD itself change how information is processed? In either case, the role of motor-related cortical activity seems likely to have to be understood both in terms of effects on the subcortical feedback systems for movement (described in section 1.6) and from the point of view of the question: what neural computations result in a mapping from motor-related goals to the patterns of activity such as the various lateralization measures?

## 3.2 Conclusions

A number of conclusions can be drawn from the studies, concerning the following questions. Can preparatory effects be found on time - frequency domain measures? Do such measures provide important extra information over ERP's? Under what conditions in task switching does oscillatory activity occur in the theta, alpha and beta bands? Can EEG data be used to study questions on task switching, e.g. is there evidence for a fallible preparatory switching process [47] (section 1.2)? What kind of brain activity is involved in motor preparation outside of the task switching context? The following sections discuss the conclusions that can be drawn from the studies, and the studies' limitations.

### 3.2.1 EEG measures

The studies explored preparatory brain activity, using a number of EEG measures. The measures - ERP's, LRP's, instantaneous amplitude and phase-locking - were sensitive to the various experimental manipulations. Further, the measures were dissociable from each other. Some contrasts affected time-domain measures but not frequency-domain measures of lateralization, such as the fast - slow by switch - hold interaction in the hand - modality switching study. So including these measures in EEG studies seems to be worthwhile, both because they do capture some aspect of brain activity and because they may provide additional physiological information from which to draw (psychological) conclusions. A very general conclusion is that brain activity in the studied contexts does indeed involve changes in large-scale frequency-domain behavior. Further, the data emphasized the importance of measures aimed at non-stationary signals: effects often involved transient increases, decreases, peaks and troughs in frequency-domain measures.

There are two important limitations in the analyses of the present studies. First, many more measures of EEG activity exist than oscillatory amplitude and the PLV. Non-linear couplings, for instance where an increase in the level of activity in one channel is associated with an increase of the frequency of oscillations in another, would not be detected using the PLV; neither would consistently coupled changes in amplitude in different frequency bands. Further, the PLV is sensitive only to consistent phase differences at equivalent time points over trials. It could be that phase-locking occurs over a certain period on each trial, but with arbitrary phase differences [124], and such phase locking, which is perhaps closer to what would intuitively be understood by the term, would require other methods [125] than the PLV to be detected. Finally, the gamma band may well contain an important part of brain activity [228]. Unfortunately, it also contains much activity due to muscle artefacts (visible in the response-speed contrast in the hand-modality switching task, section 2.1) and the development of reliable artefact removal seems to be required or at least desirable for EEG data to be analyzed in this band (see below).

Also, in the current analyses no attempt was made to determine directionality between channels, i.e. whether activity in channel A could be said to cause that in channel B more than vice versa. Directionality must be defined in terms of some model that is then fitted to the data, e.g. Granger causality is a definition of causality, and directionality, that defines the statement "A causes B" as "the present of B is predicted by the past of A". Techniques such as structural equation modelling and the directed transfer function [9] have been used to search for such relations between time series with high temporal resolution, such as the EEG. Such studies may reveal more details of the mechanisms of hierarchies of control, such as the dependence in the prefrontal cortex of stimulus on context on episodic information [119] (section 1.3.2). Note, however, that control and causality

are not synonymous: all the steps in the controlled process are causal, as are automatic processes. Measuring control would seem to require correlating activity and error reduction, not past and present.

A general problem that remains with measures in explorative studies is that the number of possible analysis techniques is infinite. More detailed hypotheses on brain processes could provide more specific predictions in terms of relations in the data. This would also reduce the statistical problems of testing "everything by everything".

The second type of limitation is that of spatial resolution. Analyses in the present studies concerned individual channels or clusters of channels, not underlying sources, as could be looked for using source localization [236] [81], or statistically well-defined components such as provided by independent component analysis [96] (ICA). ICA may also provide a solution to the problem of muscle artefacts, if such activity can be cleanly separated from that from neural sources. Building on the characteristics of and experimental effects on the measures that were found in the present studies, further research could introduce more sophisticated analyses to improve spatial resolution. For instance, coherence data between scalp electrodes can be used to estimate underlying coherence between points on a grid of locations in the brain and a given reference, using Dynamic Imaging of Coherent Sources (DICS [81]). Source localization may also provide information on the relation between lateralized beta-band ERD and phase locking: are the locked underlying sources, if phase locking between sources is in fact the cause of the phase locking between channels, the same as the sources undergoing ERD? Describing the data using sources or components would further reduce statistical problems, given reliable sources. Integration with anatomical, in vivo and other neuroimaging results would of course be improved with measures related to brain regions as opposed to scalp positions.

### 3.2.2 Preparatory activity and processes

Although further study is clearly needed before confident generalizations can be made, the data provide some suggestions on processes underlying behavior, and vice versa, the behavioral contexts in which activity was found provide suggestions on the function of that activity. In the switching studies, the most important result is that preparing to switch tasks is associated with a different pattern of brain activity than preparing for a repeated task. Further, interactions on the ERP and LRP were found between response speed and trial type (alternation versus repetition). This would appear to support the general idea that preparing for switch trials is "special", although not what the precise nature of this preparation is or whether the difference should be described as some kind of additional "switch" process (i.e. endogenous reconfiguration [197]) that is absent for hold trials. It is possible for instance that at some level of description, for both switch and hold trials, a goal must be retrieved from memory, but that the consequence of retrieval (e.g. some form of internal conflict) is different in the switch and hold contexts. Some speculations on what preparatory processes might underlie the measures pre-stimulus activity are given below.

In the hand-modality switching task, pre-stimulus theta-band amplitude was higher for fast trials, regardless of whether a switch was necessary. Other pre-stimulus activity - lateralized phase locking - was related to whether a switch was necessary, but not to response speed. The CNV showed an interaction between response speed and switching. Such results illustrate the complex nature of preparation. Preparation, defined as that which improves subsequent performance, may constitute recalling what must be prepared; overcoming the effects of a no-longer correct task set; changing the sensitivity of responses to different modalities; preventing a set of responses from



being given; or reducing noise in a goal-directed state that would cause slowness or errors. The present studies suggest, as would be expected from the literature discussed in the introduction, that the physical events that result in prepared behavior involve both rate and phase coding. Although clearly more research is needed, some speculative and badly specified assignments can be made, that may be useful in generating more specific hypotheses. Extrapolating from the present data, large-scale phase locking may be part of the way goals are encoded, or equivalently, of how the error signal for cognitive control is defined neurally. The reduction of that error signal appears to involve local oscillatory behavior, e.g. bursts of theta or periods of mu- and beta-band ERD. Elevated firing rates may be the bottom line behavior, encoding specific responses or codes in associative cortex. Pre-stimulus theta-band activity could be hypothesized to provide an autoassociative form of noise reduction, every burst of activity providing an iteration analogous to the behavior of a Hopfield network. Such a process could be one aspect of preparation: error reduction in the context of a task set implementation, nested in other processes that define what constitutes "error".

The theta-band bursts found preceding switch trials in the modality- and chiasitic-switching tasks appeared to reflect a preparatory switching process. It was hypothesized that such bursts reflect periods in which different patterns of activity compete, so that the cessation of increased EEG amplitude would indicate the resolution of competition between task sets. An association between a switch in activity and a burst of oscillatory activity occurs in the simplified model of switching illustrated in figure 3.1. In this model, a switch is made from one to another population of neurons. The mechanism is based on the most active population receiving most recurrent inhibition when the switch is triggered. The switch "command" consists only of indiscriminate excitatory input, of which the concrete effect depends on this lower-level toggling mechanism (a similar mechanism was used to allow gating in a model of prefrontal context-sensitivity, in which a network learned to perform a continuous performance ("AX") task [27]).

Only preliminary modelling work, based on the integrate-and-fire neurons used in Wang [237], was done using the described architecture. However, in a simulation of the effect of common inhibition on competition, a short period of input did evoke a period of simultaneous oscillations in a set of sub-populations (figure 3.2). The dual oscillation continued for a certain period after the command had been given, i.e., after the excitation stopped. After a number of cycles of recurrent inhibition, one population evoked recurrent inhibition before enough neurons in the other population fired to ensure its survival into the next cycle, so that in the end only one population remained active. So, as in the hypothesis concerning what association bursts of oscillatory activity could have with task switching, the resolution of the period of competition was marked by a reduction in the summed oscillatory activity.

The model illustrates a number of points. First, an unspecified switch command can be transformed into a shift of patterns of activity that is more complex than the command itself. This could be termed a "blind switch", or "abstract switch command": the population responsible for the reorganization of activity, from population A to population B, does not need to "know" about A or B; it simply says "switch" and what happens in terms of A and B is determined locally. This is only intended to illustrate the feasibility of the existence of a blind switching mechanism, but the general idea does agree with the WwM hypothesis and associated literature described in section 1.3. Second, the model provides an example of a hypothetical switching criterion in neural terms: the relative activity, or stability, of a subset of activity is the measure used to determine what gets switched. Third, the model illustrates a separation between the initiation of a switch - in this case the firing of the switch population - and subsequent processes needed for the switch com-

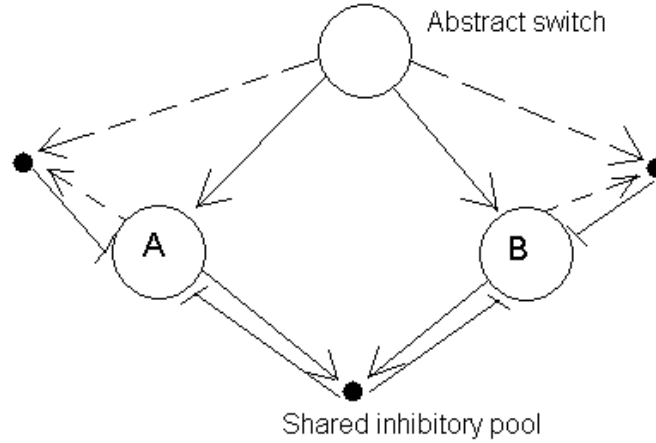


Figure 3.1: A simplified switching model. Arrows and "T"-connections represent excitatory and inhibitory connections, respectively. Strong and weak connections are plotted as continuous and dashed lines, respectively. Circles represent uniform populations of excitatory or inhibitory neurons. Connections between and within populations include both fast (AMPA) and slow (NMDA) synaptic dynamics, as in Wang [237]. With slow-dynamic synapses, recurrent inhibition results in an ongoing oscillation (section 1.1.4). Due to the lateral inhibition, if sufficient neurons in population, e.g., A fire to evokes an inhibitory pulse back to itself and B, before sufficient neurons within B fire to excite itself so that firing occurs after inhibition stops, only A will continue to fire. The unshared inhibitory pools require excitation from both the connected excitatory population and the abstract "switch-command" population to fire. So, only the currently active population will undergo inhibition when the command pulse is given. This serves as a toggling, weak-to-strong mechanism.

mand to have an effect - the competition during the period of simultaneous oscillation. Finally, the model illustrates, in an embryonic way, how behavioral patterns could be explained via relatively large-scale neural structures and processes.

Some points are also illustrated by absences in the model. How for instance are the populations being switched between defined flexibly? What triggers the switch command? How is that trigger set from instructions? Modelling work seems necessary to provide satisfactory answers to such questions in computational terms, as well as explicit causal processes that can be mapped to the anatomy and physiology of the nervous system [27]. As discussed in section 1.2, models of task switching can be used to challenge assumptions and conclusions thought to be implied by data [70]. Models that specify functions for oscillatory activity [237] [101] and phase coding [94] are especially relevant to time - frequency domain data, and by extension, to the behavioral contexts in which effects in such data are found.

A limitation of the current task switching studies is that not all combinations of manipulations were tested. Ideally, different types of cueing (alternating runs, explicit task cues, explicit switch - hold cues) would be crossed with different types of switch (modality, effector, chiastic, combinations). Further, many questions on task switching remain unanswered. For instance, if it exists, how is the command to switch embedded in memory? How are instructions transformed into task

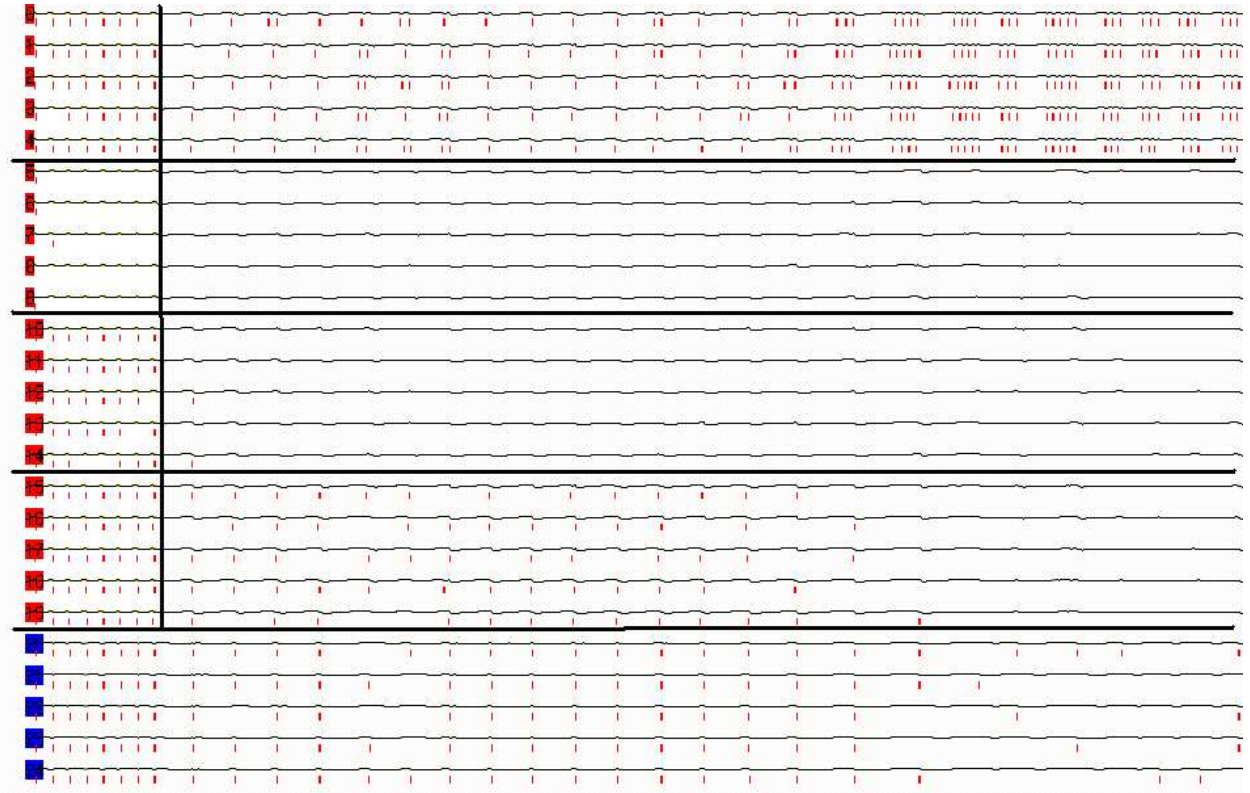


Figure 3.2: An example of the behavior of the implemented common-inhibition competition. In this model, four groups of five excitatory neurons were made, which were all-to-all connected internally, via both AMPA and NMDA synapses, but had no between-group connections. The top twenty lines show the time course (2000 ms) of the membrane potentials of the four clusters, separated by thick lines. Vertical dash marks indicate spikes. All neurons in the four excitatory groups excited the same inhibitory population (the bottom five lines), which projected back onto all the excitatory neurons. Excitatory input (as in the "switch command") was applied to the excitatory groups from the start of the plotted period up to the vertical thick line. Three of the four groups fire due to the input, which results in an oscillation due to recurrent inhibition. After the input is removed, the competition phase starts. One population loses immediately, while two populations remain active until finally only one remains, locked in the recurrent inhibition oscillation and so periodically causing the losing populations to continue to be inhibited.

sets and switching? How is long-term memory used to perform a novel task? Such questions may also benefit from combined biological - computational thinking, as computational work forces concepts to be explicitly defined and can propose causal mechanisms, while biological results provide an evolutionary grounding and possibly highly relevant fields of anatomical and physiological data (as was discussed in, e.g., sections 1.3.2 and 1.4.3).

The data concerning motor preparation suggest that different kinds of, especially beta band, activity are involved in levels of some kind of motor hierarchy. Lateralized phase locking was found when subjects knew that they would have to use the left or right hand. This occurred without significant modulation by whether responses would be fast or slow, whether a task switch was

necessary, what kind of response sequence was cued or whether there was a chance no response would be necessary at all. Lateralized ERD was also insensitive to response speed, but was dependent on task switching, response sequence and, although relatively subtly, to go probability. The LRP, finally, was most sensitive to conditions, depending on response speed, task switching, response sequence and go probability. This "nestedness", of local time domain in local frequency domain in relational frequency domain activity, could be described as following a hierarchy from knowing to doing. The further from rate coding the type of activity, the more indirect the relation to specific, overt movements seems to be. This would suggest that "higher" cognition (e.g. working memory functions as opposed to low-level visual processing) in the brain is not mapped to certain locations, but to certain distributed states, as would be expected from the literature reviewed in section 1.3. In that case, part of the function of organizational regions would appear to be setting up widespread states, in terms of types of activity, under certain learned circumstances.

In conclusion, more work is needed to construct better hypothetical models, from which observed patterns of behavior to be explained emerge, and in which computational principles are shown to be implemented in biologically based structures and mechanisms. Such models should provide testable predictions about brain activity, which would hopefully progress to become more and more explicit and detailed. An important class of models would seem to be those that relate changes in information processing to goals. Goals may coexist at different time scales, and as illustrated by the tower of hanoi, or missionary and cannibal type of problems, conflicts may occur between goals at different time scales. Understanding how such goals may conflict may provide insight in psychologically or clinically relevant behavior, for instance when people are unable to put aside short-term profits to achieve long-term goals. The neuroscientific component of the study of such goals would seem to be likely to involve the temporal gradient in the prefrontal cortex described in section 1.3.2. A further possible conflict between types of goals would be between explicit and implicit goals, for instance as seems to be the case in task switching: there is an explicit, or conscious, verbalizable goal concerning stimulus - response mappings, but an implicit, unconscious goal of the brain to achieve stability. The assumption that the brain is always attempting to achieve some goal, even if it fails to achieve goal-directed behavior, may help understand insanity [126]. Two main questions appear to lie at the basis of studying goal-directed behavior and processes. First, what is the error signal, i.e. what is being controlled - pleasant perceptual input? Maximal behavioral rest, as in Freud's secondary process? Can we consciously control internal states implementing stimulus - response mappings, as opposed to their perceived consequences, directly? Perhaps through symbolic thought, e.g. language [154]? Second, what are the automatic processes being controlled? It seems likely that understanding control, that is always "control of X", can never be understood better than the controlled processes. This bottom-up consideration also seems important from an evolutionary perspective, as presumably control could only evolve after less flexible and conditional patterns of behavior. Work on evolutionary explanations of the nervous system's development seems likely to help work on understanding what the mind is now, as well as the converse.

The present studies show that time - frequency domain analyses of preparatory activity reveal a potentially important part of brain activity involved in such goal implementation and goal conflicts. So, however the brain organizes itself to achieve cognitive control, complete hypotheses on this organization should include large-scale patterns of oscillatory neural behavior and its functional roles. The existence of organizational principles on relatively large scales may be a necessary and sufficient condition for the reliable construction of a "mid-level" language of brain activity,

in which objects consist of patterns of neural activity, emerging from many neuronal interactions between brain structures and resulting in behavior aimed at interacting with the world. Such a language would provide a link between the behavior of individual or small groups of neurons and psychological constructs aimed at explaining overt behavior. Discovering / constructing this language, as is being done in e.g. modelling work discussed in previous sections [237] [27] [54], would seem to require a close partnership between empirical (especially psychological and biological) and theoretical (especially mathematical) study.